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Impact of eutrophication and river management within a framework of ecosystem theories

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Abstract

Eutrophication became a dominant process in the Mondego estuarine system in the 1980s, presumably as a result of excessive nutrient release into coastal waters. The main symptoms were the occurrence of seasonal blooms of *Enteromorpha* spp., green macroalgae, and a drastic reduction of the *Zostera noltii* meadows. Previous results suggest that this process will determine changes in species composition at other trophic levels. This paper aims at integrating the available information to provide a theoretical interpretation of the recent physicochemical and biological changes in the Mondego estuarine ecosystem, which will be further used as basic framework for the development of a structurally dynamic model. Exergy-based indices, the Exergy Index and Specific Exergy, were applied as ecological indicators (orientors) to describe the state of the ecosystem, taking into account different scenarios along a spatial gradient of eutrophication symptoms. This allowed elucidating the present conditions along the spatial gradient as representing various stages in the temporal evolution of the system, within the framework of *bifurcation*, Chaos, and Catastrophe theories. Eutrophication appeared as the major driving force behind the gradual shift in primary producers from a community dominated by rooted macrophytes (*Z. noltii*) to a community dominated by green macroalgae. Through time, concomitant changes at other trophic levels will most probably give origin to a new trophic structure. Moreover, river management emerged as a key question in establishing scenarios in order to determine secondary effects in eutrophied systems. Results suggest that a more conservative river management may be used as a powerful tool to remedy affected areas, including the implementation of ecological engineering principles in different possible management practices. The recent biological changes in the Mondego estuarine ecosystem were found to comply with the framework of the theories considered, while both Exergy-based indices were able to capture the state of the system and distinguish between different scenarios.

Keywords: Estuary; Biological communities; Stress-induced changes; Ecological indicators; Ecosystem theories

1. Introduction

The Mondego River drains a hydrological basin of approximately 6670 km^2. Its estuary, located in the western coast of Portugal, is the location of a

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mercantile harbour (Figueira da Foz). Besides the harbour facilities, the estuary supports industrial activities, salt-works, and aquaculture farms. Additionally, the lower Mondego River valley consists of 15,000 ha of farming fields (mainly for rice production), which supply an important input of nutrients into estuarine waters (Marques et al., 1993a; Pardal et al., 2000; Martins et al., 2001).

The Mondego estuary is located in a warm temperate region with a basic mediterranean temperate climate. It consists of two arms, north and south (Fig. 1).

The two arms become separated by an island at the estuarine upstream area, at about 7 km from the sea, and join again near the mouth. The two arms of the estuary exhibit very different hydrographic characteristics. The north arm is deeper (5–10 m during high tide, tidal range about 2–3 m), while the south arm (2–4 m deep, during high tide) is almost silted up in the upstream areas, which causes the freshwater of the river to flow essentially through the north arm. Actually, the water circulation in the south arm is mostly due to tides and to the freshwater input of a tributary, the Pranto River, which is artificially controlled by a sluice, located at 3 km from the confluence with the south arm of the estuary (Fig. 1). In addition, due to differences in depth, the penetration of the tide is faster

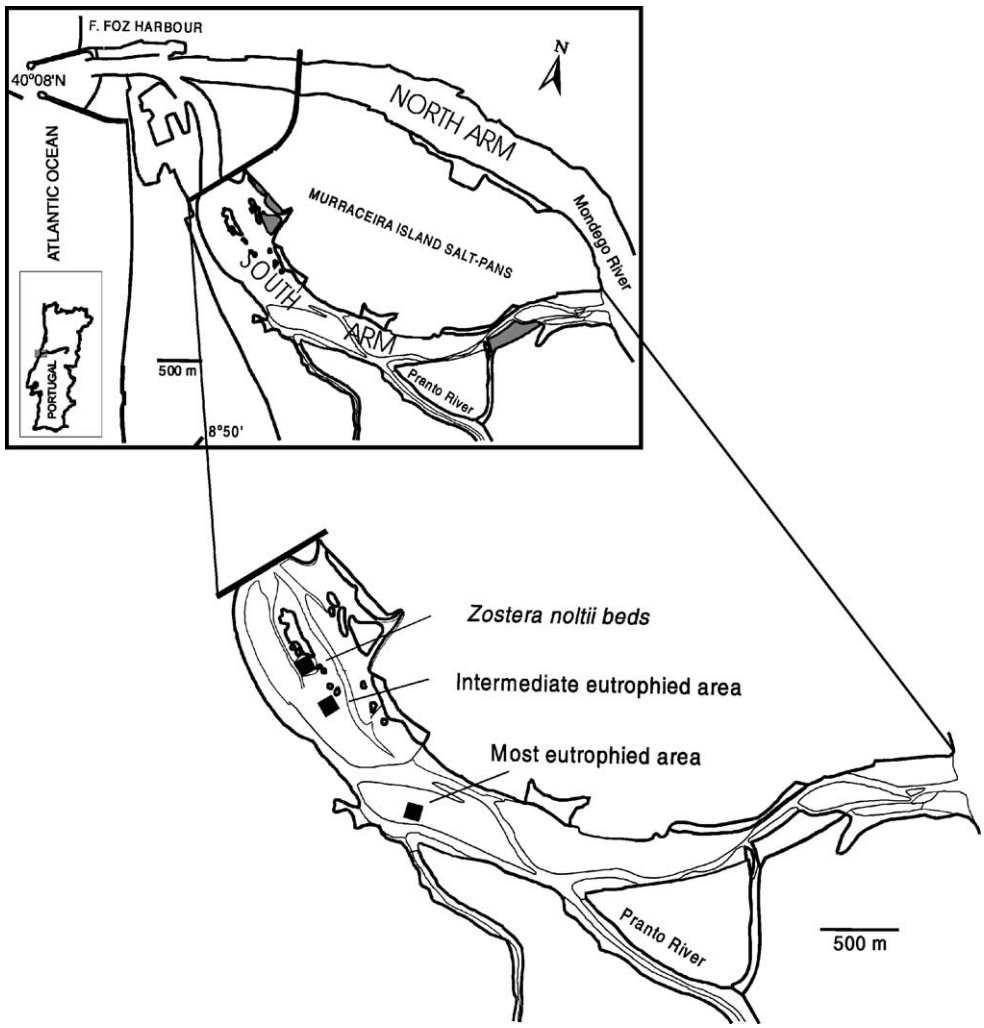

Fig. 1. Location of the three sampling stations along a spatial gradient of eutrophication in the south arm of the Mondego estuary.

in the north arm, causing daily changes in salinity to be much stronger, whereas daily temperature changes are higher in the south arm (Marques et al., 1993a).

In both arms of the estuary, hard substrates are primarily covered by *Enteromorpha* spp. and *Fucus* spp., which constitute eulittoral macroalgae belts, although in the upper limit of the sublittoral zone *Ulva* spp. also occurs. Hard substrates are essentially due to human occupation (e.g. harbour facilities, aquaculture farms, saltworks), and extend at least along 60% of the estuarine perimeter. Especially in the north arm, salt marshes of *Spartina maritima* and *Zostera noltii* meadows have been gradually replaced by hard substrate habitats primarily covered by the brown algae *Fucus vesiculosus* (personal observation). Nevertheless, in the south arm, most of the intertidal zone still consists of soft substrates, from sand to mud, where *S. maritima* marshes and *Z. noltii* beds could constitute significant populations (Marques et al., 1993b; Flindt et al., 1997).

As in most estuaries all over the world, eutrophication largely increased in the Mondego estuarine system since the 1980s, presumably as a result of excessive nutrients release into coastal waters. The most visible feature of eutrophication in the Mondego estuary is the occurrence of seasonal green macroalgae blooms (mainly of *Enteromorpha* spp.), which have been reported in the south arm for several years (Marques et al., 1993a,b, 1997; Flindt et al., 1997). The *Z. noltii* beds, which represent the richest habitat with regard to productivity and biodiversity (Marques et al., 1993b, 1997), have been drastically reduced in the south arm of the Mondego estuary, most likely as a function of competition with *Enteromorpha* (Raffaelli et al., 1991; Hodgkin and Hamilton, 1993), resulting from the different strategies of macroalgae and macrophytes to uptake nutrients, and also from the shading effects of macroalgae on macrophytes (Hardy et al., 1993; Hartog, 1994). Actually, in the beginning of the 1980s, the *Z. noltii* beds covered a large fraction of the intertidal area, extending to the upstream section of the south arm, along the Murraceira Island (Fig. 1) (personal observation), while by the end of the 1990s this species distribution was restricted to its downstream section.

Usually, macroalgae blooms (especially in the inner areas of the south arm of the estuary) occur from late winter to an early summer peak when an algae collapse may take place (Marques et al., 1997; Lillebø et al., 1999; Pardal et al., 2000). During macroalgae blooms, the concentration of dissolved oxygen increases significantly during the day, which is obviously related to primary production, becoming extremely low during the night, due to algae biomass respiration (Martins et al., 1997). This diurnal cycle probably explains the occurrence of the algae crashes described above (Flindt et al., 1997; Martins et al., 2001). Nevertheless, the annual biomass of *Enteromorpha* spp., and therefore blooms occurrence, appears to be strongly dependent on the amount of freshwater that enters the south arm during winter and spring. In turn, the input of freshwater is regulated by precipitation and by river management practices, as a function of the water needs of rice crops located upstream from the estuary (Martins et al., 2001).

In general, it has been observed that benthic eutrophication in estuaries and coastal lagoons may determine a shift in the benthic primary producers (Lavery et al., 1991; Hartog, 1994), like the gradual replacement of *Zostera* by *Enteromorpha* observed in the Mondego (Marques et al., 1997). It is obviously reasonable to assume, and many results from research carried out in the Mondego estuary (Cabral et al., 1999; Lillebø et al., 1999; Lopes et al., 2000; Pardal et al., 2000) comply with it, that this may determine changes in species composition at other trophic levels, and through time give rise to a new trophic structure.

A recent data set, obtained from January 1993 to June 1994 in the scope of a EU research project (MAS2-CT92-0036) provided a suitable description of the temporal variation of physicochemical factors of water and sediments and of the composition of the benthic communities along the estuarine gradient of eutrophication. Such data were already made partially available in a number of publications (Flindt et al., 1997; Marques et al., 1997; Martins et al., 1997).

The main goal of this paper is to combine past observations and more recent data in an integrative manner, providing an interpretation of the recent biological modifications in the Mondego estuary ecosystem in the light of ecological theories.

Additionally, we aimed to test the Exergy Index and Specific Exergy as ecological indicators (orientors), in terms of evaluating its capability to capture the state of the system, distinguishing between different scenarios along the spatial gradient of eutrophication symptoms. These two thermodynamically oriented indicators

are derived from ecosystem theory. The application of Exergy in ecological systems was proposed in the late 1970s (Jørgensen and Mejer, 1979). In terms of its spatial and temporal patterns of variation, the properties of Exergy-based indices, respectively the Exergy Index and Specific Exergy, have been analyzed before taking into account the Mondego estuary biological communities, allowing us to test in what extent their values could elucidate about the system's characteristics (Marques et al., 1997). Nevertheless, it was concluded that both Exergy-based indices should be applied complementarily, since Specific Exergy is very sensible to abrupt changes in species composition, for instance the fast decline of green macroalgae following a bloom, while the Exergy Index appears to capture well slower modifications (Marques et al., 1997). The objective here is to examine if, despite some differences in their responses, the variations of these ecological indicators along the spatial gradient of eutrophication symptoms were consistent with our theoretical interpretation of the system's development. The application of these indicators may be based on a model, see for instance Jørgensen et al. (2002), or based on empirical observations. In the present case, we will use the later approach. The reason for this choice is the fact that these data will be further used to calibrate a structurally dynamic model of the development of the Mondego estuary benthic communities following an eutrophication process. Structurally dynamic models are able to describe the modifications observed in the systems, namely the shift in the dominant primary producers, which in the case are being induced by eutrophication. In this model, these indicators will be used as orientors to the model dynamics. Therefore, it would be necessary to verify if the Exergy Index and Specific Exergy are able to capture the system properties before the model is developed. A preliminary version of the model is presented in Jørgensen et al. (2002), and further developments must be preceded by the necessary theoretical assumptions.

One method to implement structurally dynamic models is to use goal functions. Goal functions are mathematical algorithms, which act as ecological indicators, constituting emergent properties arising from self-organization processes of development. In structurally dynamic models parameters are allowed to change as a function of forcing functions and state variables. Exergy-based ecological indicators appear to be very promising goal functions, showing a possible role in expressing shifts in species composition and trophic structure in shallow lakes ecosystems. For details on this application see for instance Jørgensen (1997).

2. Materials and methods

2.1. Data collection

Physicochemical factors of water and sediments and the macrobenthic communities were monitored along a spatial gradient of eutrophication symptoms in the south arm of the Mondego estuary during 18 months, from January 1993 to July 1994. Samples of macrophytes, macroalgae, and associated macrofauna were taken fortnightly at three different sites, during low water, along an estuarine gradient of eutrophication in the south arm of the estuary (Fig. 1). Sites considered were (a) a non-eutrophied zone, where a macrophytes community (*Z. noltii*) is present; (b) an intermediate eutrophied area, where roots can still be found in the sediment, although macrophytes are not present anymore, and where green macroalgae reach a significant development; and (c) a heavily eutrophied zone, in the inner areas of the estuary, from where vestiges of the former presence of macrophytes totally disappeared, while *Enteromorpha* spp. blooms have been observed during the last decade.

Biological samples were taken by using a manual corer. Each time and at each site, 10 replicates were randomly taken, each replicate corresponding to 141 cm^2 and approximately 3 l of sediment. All the biological samples were sieved in situ using a 1 mm mesh size sieve, and then fixed in 4% neutralized formaldehyde. This mesh size was considered suitable for this study, regarding the types of sediment we expected to find along the estuary. Simultaneously, corresponding to biological samples, water, salinity ($g\,l^{-1}$), temperature (°C), pH, and oxygen dissolved were measured in situ. Ammonia, silica, chlorophyll a, nitrites, nitrates, and phosphates ($mg\,l^{-1}$) were determined in the laboratory from water samples. Sediment samples were also collected and subsequently analyzed for granulometry and organic matter contents ($g\,m^{-2}$ afdw—ash free dry weight).

The organisms collected (macrophytes, macroalgae, and macroinvertebrates) were separated, preserved in 70% ethanol or in 4% neutralized formaldehyde, according to the presence or absence of calcareous parts, further identified, almost always to the species level, and their biomass determined ($g\,m^{-2}$ afdw).

To provide a more general description regarding the variation of the characteristics of macrobenthic communities along the spatial gradient of eutrophication symptoms, data on its composition was pooled as a function of higher taxa and functional groups. Six higher taxonomic levels were considered, respectively Gastropods, Bivalves, Polychaetes, Amphipods, Isopods, and others. On the other hand, four functional groups were considered Herbivores, Detritivores, Carnivores, and Omnivores, respectively.

In order to analyse the effects of the freshwater discharge from mainland on the water quality and to estimate the nutrients loading into the south arm of the estuary a monitoring program was carried out on at the Pranto River sluice (Fig. 1) (Flindt et al., 1997). As explained above, this sluice is used for water management, controlling the freshwater discharge from this tributary and avoiding the penetration of tidal saltwater in rice fields located upstream. During each opening of the sluice, the amount of water discharged was quantified and the concentration of nutrients determined each hour (Flindt et al., 1997).

2.2. Exergy Index and Specific Exergy estimations

Exergy is a concept derived from thermodynamics that may be seen as energy with a built in measure of quality. Exergy is a measure of the distance between a given state of an ecosystem and what the system would be at thermodynamic equilibrium (Jørgensen and Mejer, 1979). In other words, if an ecosystem were in equilibrium with the surrounding environment its Exergy would be zero. This means that, during ecological succession, Exergy is used to build up biomass, which in turn stores Exergy.

In thermodynamic terms, taking an ecosystem's trophic structure as a whole, there will be a continuous modification of the structure as a function of changes in the prevailing environmental conditions, during which Exergy storage will be optimized (Jørgensen, 1997). In other words, ecological succession drives from more simple to more complex ecosystems, which seem at a given point to reach a sort of balance between keeping a given structure, emerging for the optimal use of the available resources, and modifying the structure, adapting it to a permanently changing environment. For a more detailed description of this concept see for instance Jørgensen (1997).

The Exergy of a system compared with the same system at the same temperature and pressure but in the form of an inorganic soup without any life, biological structure, information or organic molecules can be computed from (Jørgensen and Mejer, 1979; Jørgensen, 1997):

$$\mathrm{Ex} = RT\sum_{i=0}^{n} C_i \ln\frac{C_i}{C_{i_{\mathrm{eq}}}}$$

where R is the gas constant, T is the absolute temperature, C_i is the concentration in the system of component i, $C_{i_{\mathrm{eq}}}$ is the corresponding concentration of component i at thermodynamic equilibrium, n is the number of components, and index 0 indicates the inorganic compounds of the considered element. $C_{i_{\mathrm{eq}}}$ is of course a very small concentration (except for $i = 0$, which is considered to cover the inorganic compounds), corresponding to a very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium.

In ecological terms, the above formulation is not practical due to the obvious difficulties in determining the reference level for a given compartment of the system. An approximate estimation of Exergy may nevertheless be obtained following the approach proposed by Jørgensen et al. (1995):

$$\mathrm{Ex} = \sum_{i=1}^{n} \beta_i C_i$$

where C_i is the concentration in the ecosystem of component i (e.g. biomass of a given taxonomic group or functional group) and β_i expresses roughly the quantity of information embedded in the biomass. Detritus is chosen as reference level, i.e. $\beta_i = 1$, and Exergy in biomass of different types of organisms is expressed in detritus energy equivalents.

The outcome of such estimation does not correspond anymore to Exergy in the strict thermodynamic

sense, and is therefore called an Exergy Index (Jørgensen, 1997; Marques et al., 1997). This index has been tested as ecological indicator by Marques et al. (1997).

Through time, the variation of Exergy in an ecosystem may, therefore, be considered as equal to the variation of the biomass plus the information built in one unit of biomass (expressing the quality of the biomass):

$$\Delta \mathrm{Ex}_{\mathrm{tot}} = \Delta \mathrm{Biom}\, \beta_i + \Delta \beta_i\, \mathrm{Biom}$$

If the total biomass ($\mathrm{Biom}_{\mathrm{tot}}$) in the system remains constant through time, then the variation of Exergy (Ex) will be a function of only the structural complexity of the biomass or, in other words, of the information embedded in the biomass, which may be called Specific Exergy (SpEx), or Exergy per unit of biomass.

Table 1
Values for the weighting factors to estimate Exergy related to organisms biomass for different groups of organisms

Organisms	Weighing factor
Detritus	1
Minimal cell	2.7
Bacteria	3.0
Algae	3.9
Yeast	6.4
Fungus	10.2
Sponges	30
Moulds	32
Plants, trees	30–87
Jellyfish	30
Annelid worms	50
Insects	70
Crustacean Zooplankton	30–46
Crustaceans (Decapods)	230
Gastropods	450
Bivalves	760
Echinoderms	260
Fish	287–344
Amphibians	800
Reptiles	1000
Birds	1100
Mammals	1300

Values of weighting factors are based on the number of information genes. The Exergy content of the organic matter in the various organisms is compared with Exergy contained in detritus. Estimations were carried out according to the method described by Jørgensen et al. (1995), based on analytical work (Fonseca et al., 2000) and on literature sources (Lewin, 1994; Li and Grauer, 1991).

Specific Exergy represents, therefore, a measure that takes into account how well an ecosystem uses the available resources, independently from the amount of resources. For each instant, Specific Exergy is given by:

$$\mathrm{SpEx} = \frac{\mathrm{Ex}}{\mathrm{Biom}_{\mathrm{tot}}}$$

The Exergy Index and Specific Exergy were calculated from the biomass of the different organisms ($\mathrm{g\,m^{-2}}$ afdw) through the use of weighting factors able to discriminate different "qualities" of biomass (Table 1). For this purpose, taking into account the available set of weighting factors, data on organism's biomass were pooled as a function of higher taxonomic levels (e.g. Phylum or Class).

3. Results

Here, we consider only the results relevant to interpret the occurrence of macroalgae blooms in relation to river management and its effects on the estuarine macrobenthic communities.

3.1. Salinity variation

Salinity is an important external factor to control the growth of *Enteromorpha intestinalis*, the most abundant green macroalgae in the Mondego estuary in terms of biomass, and therefore in conditioning the occurrence of blooms (Martins et al., 1999). In Fig. 2, we show the fortnightly variation of salinity values in the water column during low tide at the three sampling stations along the estuarine gradient of eutrophication. We relate it to the opening of the Pranto River sluice, which controls the water level in rice fields upstream from the estuary. The temporal pattern of variation was clearly identical at all stations. Salinity values ranged between 15 and 35‰ during winter, spring, and summer 1993, a dry year. All over this period the sluice was kept closed. From late summer 1993, a rainy period started and the sluice was opened in order to manage the water level in the rice fields. Salinity values decreased then significantly, ranging approximately between 5 and 20‰ and being lower than 10‰ during a considerable period in winter.

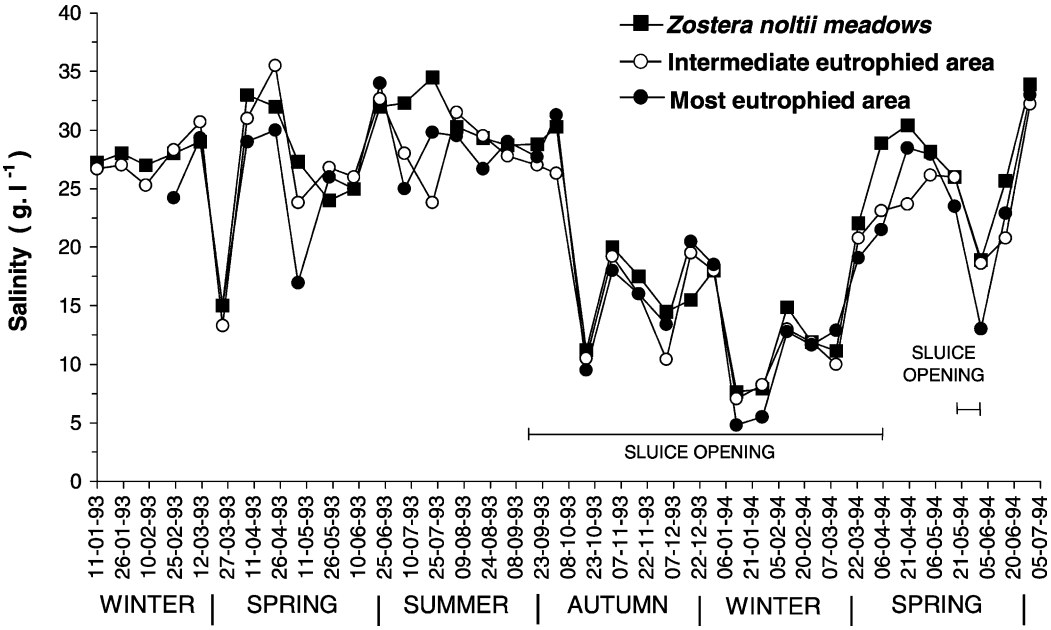

Fig. 2. Fortnightly variation of salinity at the three stations along the spatial gradient of eutrophication.

3.2. Variation of nutrients concentration in the water column

Nitrogen is usually considered a limiting factor for estuarine and marine primary production, while phosphates are normally considered as the limiting nutrient in freshwater systems, namely in mesotrophic lakes. Silica may also constitute a limiting factor for phytoplankton diatom growth, which might indirectly influence benthic filter feeders. We, therefore, considered it important to analyse the variation of these nutrient concentrations in the water column in relation to the opening of the Pranto River sluice. In Fig. 3A–E, we show the fortnightly variation of nutrient concentrations in the water column during low tide. Additionally, in Fig. 3F we show the variation of the N/P ratio in the water column. It is quite clear from the available data that silica nitrites, nitrates and ammonia concentrations exhibited a very significant increase in the water column during sluice opening at all the three sampling stations demonstrating that these nutrients, especially nitrogen, proceed from the freshwater discharge, and therefore have origin in agricultural fertilization.

On the other hand, it is also clear that phosphate concentration in the water column was significantly higher in the intermediate eutrophied area and in the most strongly eutrophied area of the system when the sluice was kept closed.

Phosphates apparently are much lower and basically similar at all the three stations when the sluice was opened. In fact, in estuarine systems, phosphates are apparently mainly released to the water column in its soluble form from the organic matter in sediments (Lijklema and Hieltjes, 1982; Sfriso et al., 1987; Valiela, 1995), becoming very much diluted in the water column when the sluice is opened and important freshwater discharges occur.

The N/P ratio in the water column also increased significantly in the water column when the sluice was opened in comparison with the periods when it was closed. This was obviously due to the combined effects of nitrogen loading into the estuary and phosphates dilution, and it is reasonable to hypothesise that during the opening of the Pranto River sluice phosphorous might become a limiting factor to primary production in the south arm of the Mondego estuary.

We may, therefore, recognize two different scenarios with regard to water quality in the system. The first 8–9 months of observations corresponded to the end of a 2-year dry period during which the

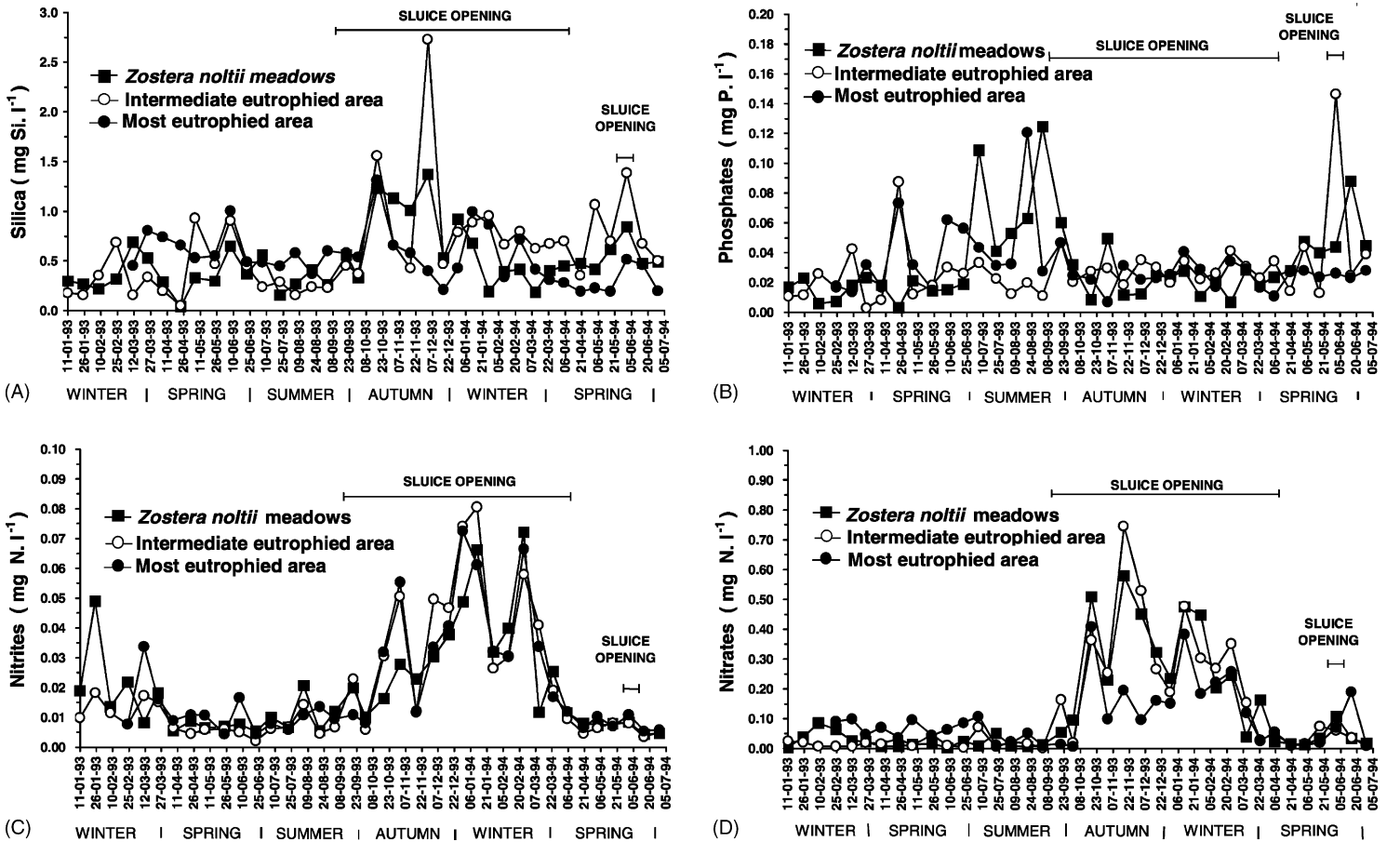

Fig. 3. Fortnightly variation of nutrients at the three stations along the gradient of eutrophication: (A) silica; (B) phosphates; (C) nitrites; (D) nitrates; (E) ammonia; (F) N/P ratio.

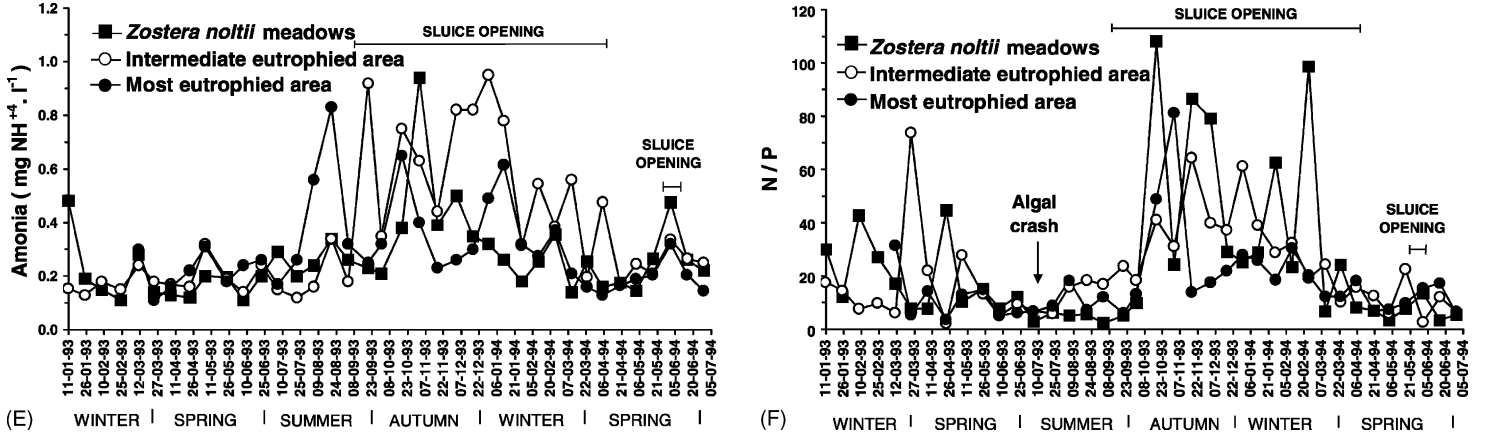

Fig. 3. (*Continued*).

Pranto River sluice was rarely opened. The subsequent period corresponded to an extremely rainy year, during which the sluice was opened almost daily. Therefore, due to water management practices, effects from precipitation are not directly reflected in the south arm of the Mondego estuarine system.

3.3. Variation of Z. noltii and macroalgae biomass

With regard to primary producer data, in the non-eutrophied area the total biomass of macrophytes suffered clear seasonal changes (Fig. 4A). During spring of 1993, there was an increase in leaf biomass. This reached a maximum of 328.4 $g\,m^{-2}$ afdw in

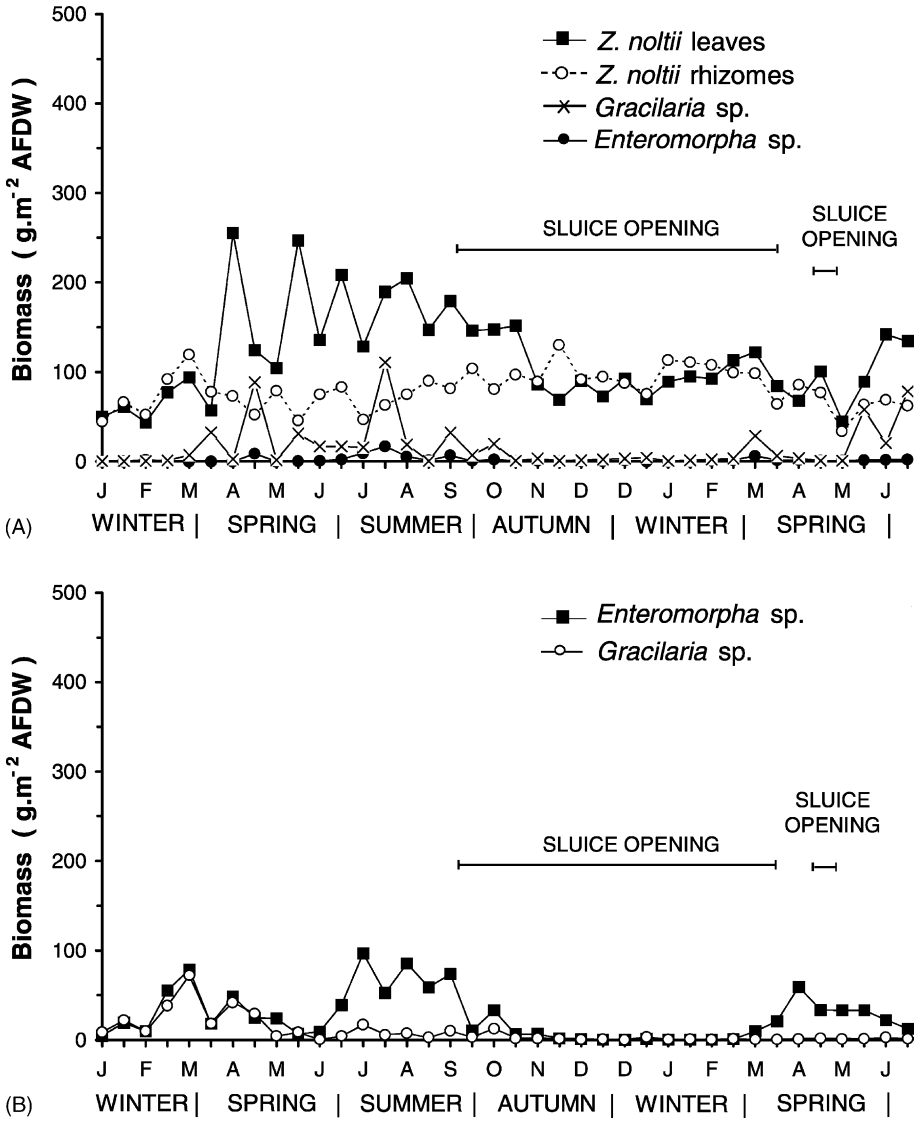

Fig. 4. Fortnightly variation of primary producers biomass at the three stations along the gradient of eutrophication: (A) *Z. noltii* beds; (B) intermediate eutrophied area; (C) most eutrophied area.

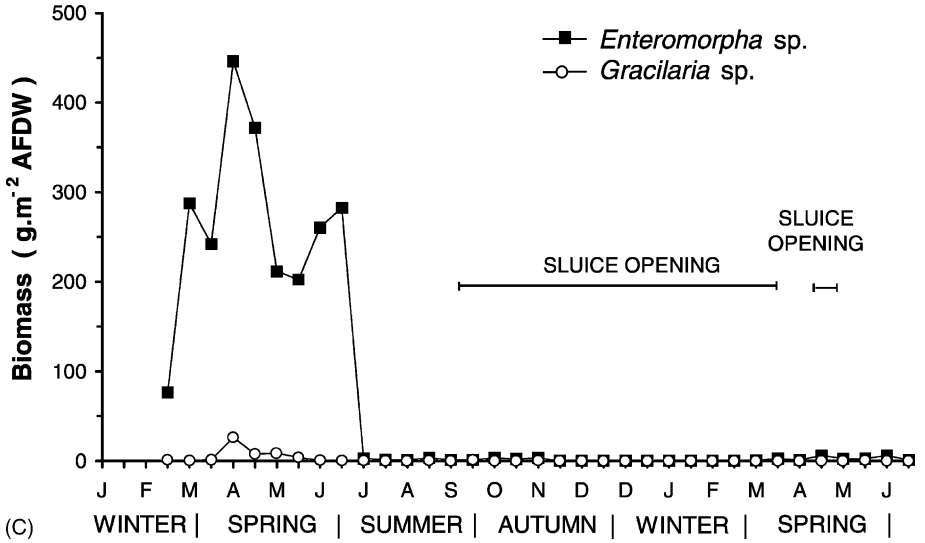

Fig. 4. (*Continued*).

April. Nevertheless, during the next spring, leaf biomass did not increase as one would expect. Rhizomes consistently presented higher biomass during fall and winter when they could even present higher values then the leaves (e.g. 130 g m^{-2} afdw in November 1993). *Z. noltii* was not found in the other two sampling stations.

With regard to macroalgae, *Gracillaria* sp. (red algae) was the most abundant one in the non-eutrophied area (Fig. 4A). The levels peak during spring and summer (maximum of 110.6 g m^{-2} afdw in July 1993) but exhibiting always much lower biomass than the macrophytes. Green macroalgae biomass, namely *Enteromorpha* spp., was always very low on the *Z. noltii* beds (maximum 16.9 g m^{-2} afdw in June 1993).

In the intermediate eutrophied area, *Gracillaria* sp. was less abundant than in the *Z. noltii* beds, while green macroalgae biomass increased substantially, reaching a maximum of 96.9 g m^{-2} afdw in July 1993 (Fig. 4B).

In the most eutrophied area, corresponding to the inner areas of the south arm, green macroalgae exhibited a bloom up to early summer 1993, reaching a maximum biomass of 413.19 g m^{-2} afdw in April 1993 (Fig. 4C). From June 1993 green macroalgae suffered a collapse and did not recover until the end of the study period. In this area, even during the green macroalgae bloom, *Gracillaria* sp. biomass was negligible.

3.4. Variation of benthic higher taxa and functional groups biomass

To provide a more general description regarding the variation of the characteristics of macrobenthic communities along the spatial gradient, data on its composition was pooled as a function of higher taxa and functional groups. Six higher taxonomic levels were considered, Gastropods, Bivalves, Polychaetes, Amphipods, Isopods, and others, respectively. On the other hand, four functional groups were considered, Herbivores, Detritivores, Carnivores, and Omnivores, respectively.

In the non-eutrophied area, corresponding to the *Z. noltii* beds (Fig. 5A), we observed a stable macrofauna composition. The most abundant groups were Gastropods, with *Hydrobia ulvae* as dominant species, and Bivalves, mainly represented by *Cerastoderma edule*. Amphipods, Isopods and Polychaetes were always much less abundant and, taking into account sampling bias, we may say that these groups basically kept their relative proportions through the study period. Others include the Decapods (Crustaceans), basically represented by *Carcinus maenas*, and the observed changes in their biomass were basically dependent on the casual capture of larger specimens. In fact, although large Decapods are normally included in what is called benthic macrofauna, they are actually

much bigger than other estuarine macrofaunal organisms. The reduction in Gastropod biomass observed in this area by the end of the study period was likely due to the severe perturbation in this habitat caused by fishermen scraping the whole area looking for bait.

In the intermediate eutrophied area (Fig. 5B), the biomass was generally lower than in the other

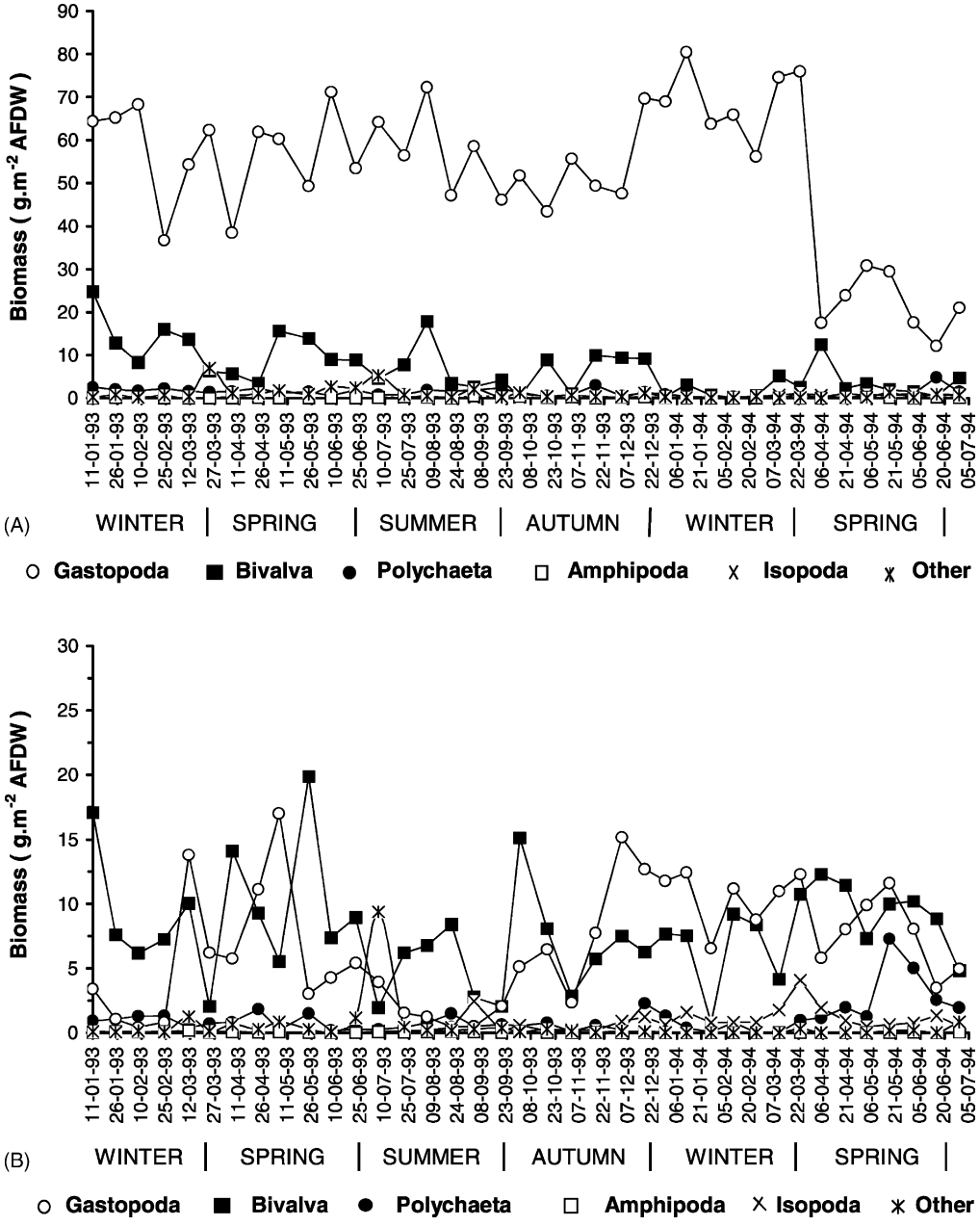

Fig. 5. Fortnightly variation of higher taxonomic groups biomass at the three stations along the gradient of eutrophication: (A) *Z. noltii* beds; (B) intermediate eutrophied area; (C) most eutrophied area.

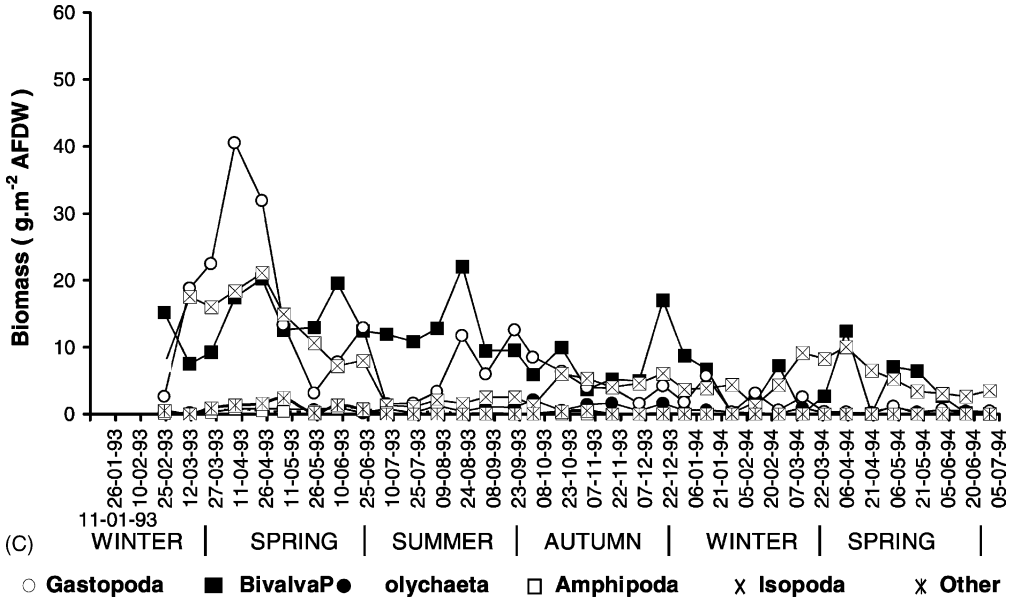

Fig. 5. (*Continued*).

sampling sites. Moreover, there was never a stable scenario regarding the composition of macrobenthic communities. From early winter to late spring in 1993, Gastropods and Bivalves alternate as dominant groups. Coinciding with the decrease of green macroalgae, Amphipods and Isopods became the dominant groups for a short period. Then there was a return to the previous scenario, with Gastropods and Bivalves alternating as dominant groups, while Polychaetes suffered a clear biomass increase during spring 1994.

In the most eutrophied area (Fig. 5C), during winter and spring 1993, corresponding to the green macroalgae bloom, Gastropods were the dominant group. On the other hand, although Bivalves were second in abundance, Amphipods and Isopods also developed quite abundant populations. In early summer 1993, the collapse of green macroalgae was followed by a drastic reduction of Gastropods, Amphipods and Isopods, while Bivalves resisted. They become the dominant group in the immediate post crash scenario, due to the presence of newly recruited individuals of *Scrobicularia plana*. Meanwhile, Isopods showed a clear recovery by the end of summer 1993 and started alternating with Bivalves in dominance, but Gastropods and Amphipods became secondary groups up to the end of the study period. Polychates also became more abundant following the disappearance of macroalgae.

We, therefore, identify two distinct periods: (i) during the green macroalgae bloom the macrofauna community was dominated by Gastropods with also abundant populations of Bivalves (mainly *Scrobicularia plana*), Amphipods, and Isopods; (ii) after the macroalgae collapse Bivalves and Isopods became the most abundant groups alternating in dominance.

With regard to functional groups, in the non-eutrophied area (Fig. 6A), all over the study period, Detritivores and Herbivores were clearly the dominant groups, taking advantage of the abundance of detritus resource provided by the decay of broken *Zostera* parts, and of grazing opportunities on epiphytes that cover *Zostera* leaves. Besides, *Zostera* leaves act as a trap for suspended sediments, and therefore for organic matter particles usable by Detritivores (Valiela, 1995). Omnivores and Carnivores are always much less abundant. Therefore, despite seasonal variations we observed the same stable pattern throughout the study period.

In the intermediate eutrophied area (Fig. 6B), the scenario appears totally distinct. Besides the fact that Detritivores are dominant most of the time and Carnivores always poorly represented, it is impossible to

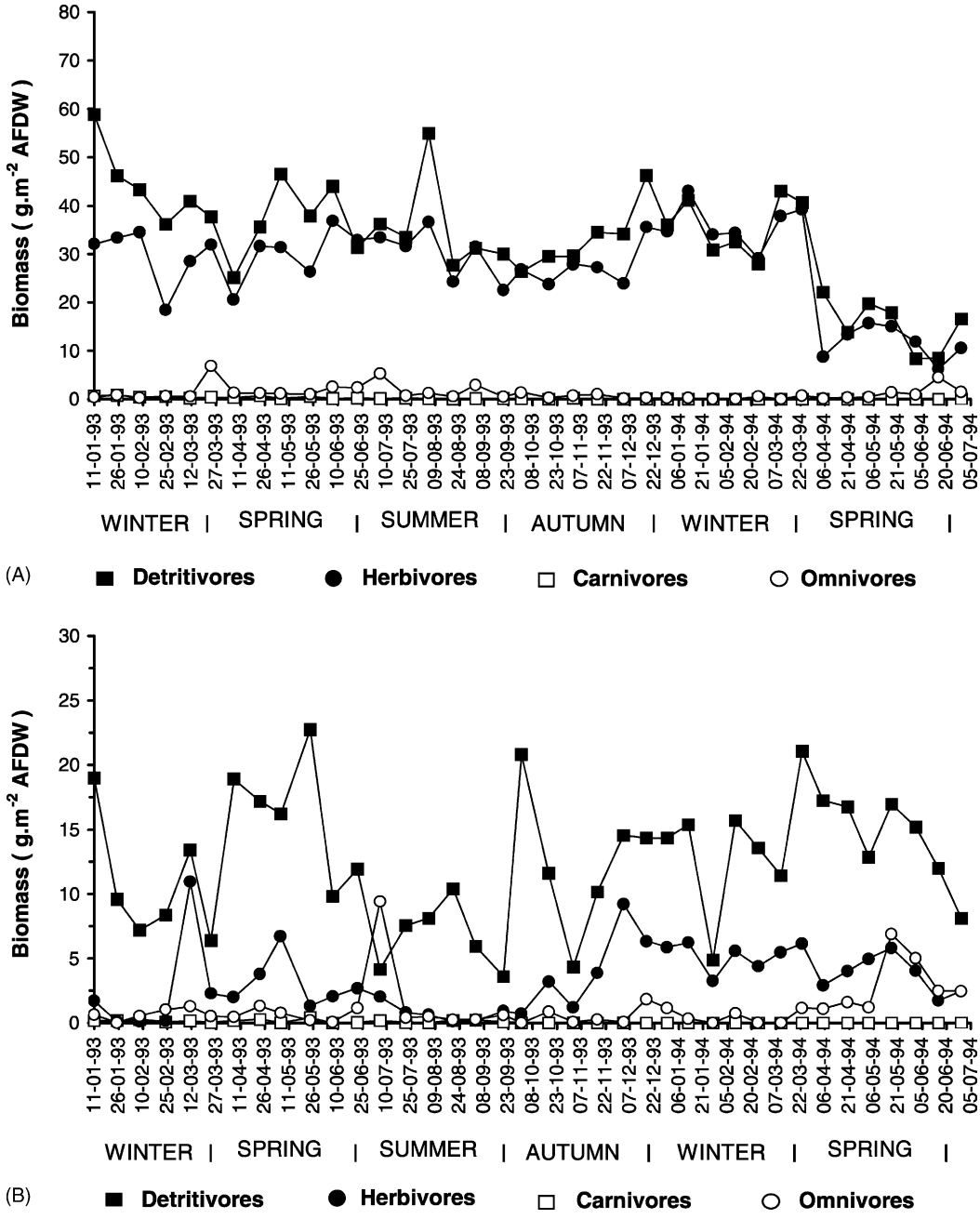

Fig. 6. Fortnightly variation of functional groups biomass at the three stations along the gradient of eutrophication: (A) *Z. noltii* beds; (B) intermediate eutrophied area; (C) most eutrophied area.

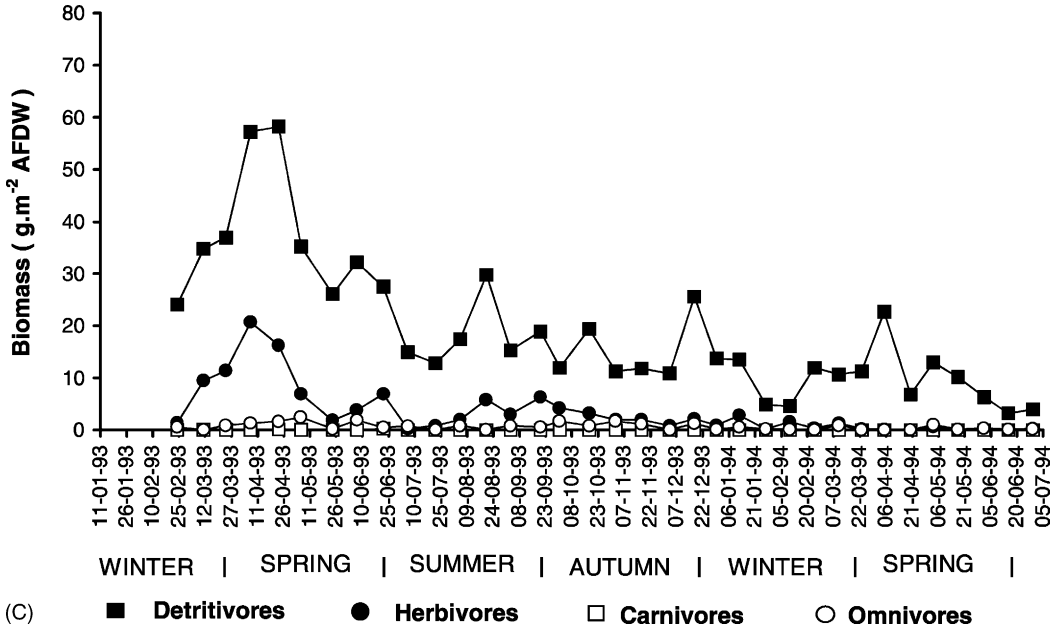

Fig. 6. (*Continued*).

recognize any pattern through the study period, since functional groups alternate very much in dominance (qualitative oscillations), which appear to correspond to a very unstable situation.

Finally, in the most eutrophied area (Fig. 6C), Detritivores are by far the dominant group through the study period, followed by Herbivores, although the biomass of both groups suffered a drastic reduction after the green macroalgae disappearance. As in the other two sampling stations, Carnivores and Omnivores are poorly represented. Therefore, from the trophic point of view, besides variations in the total biomass of each group as a function of feeding opportunities provided by the macroalgae bloom (quantitative oscillations), the scenario appears more or less stabilized in this area.

3.5. Spatial variation of the Exergy Index and Specific Exergy along the spatial gradient of eutrophication symptoms

In Table 2, we present the Exergy Index and Specific Exergy in the three areas considered along the spatial gradient. Both indicators are consistently higher in the

Table 2
Exergy Index and Specific Exergy variation in three scenarios identified along the gradient of eutrophicatiom symptoms in the south arm of the Mondego estuary

Indicator	*Z. noltii* beds (non-eutrophied area)			Intermediate eutrophied area			Most eutrophied area (*Enteromorpha* spp. dominant)		
	Average	S.D.	Range	Average	S.D.	Range	Average	S.D.	Range
Exergy Index	25389	±2533 (10%)	20143–29530	4802	±2059 (43%)	1803–7990	8553	±4485 (52%)	2688–19805
Specific Exergy	211	±28 (13%)	120–270	151	±132 (87%)	9–373	160	±95 (59%)	32–255

For each area we provide the average annual value of each indicator, the correspondent standard deviation and the range of values, based on data collected from January 11, 1993 to July 5, 1994. Exergy is expressed in $g\,m^{-2}$ detritus energy equivalents and Specific Exergy is expressed in Exergy × (Unit of biomass)$^{-1}$.

Z. noltii beds, the non-eutrophied area, followed by the areas where green macroalgae blooms take place, the high and mid eutrophied area. The range of variation, for both indicators, is smaller in the non-eutrophied area, expressing a more stable situation. Oscillations are much stronger in the other two areas, as expressed by the standard deviations and the magnitude of the variations. This is particularly evident if one takes into account Exergy Index and Specific Exergy variations in the intermediate eutrophied and in the most eutrophied areas (see also Fig. 8C and D). Meanwhile, only the Exergy Index for the *Z. noltii* beds was significantly different from the other two areas. Despite the fact that Specific Exergy variations are rather small in the *Zostera* meadows, significant differences cannot be recognized due the very strong oscillations in the other two areas, namely in the intermediate eutrophied one.

4. Discussion and tentative theoretical interpretation

Qualitative observations carried out in the Mondego estuary since the early 1980s (Marques et al., 1984) provide a general idea regarding how the system was at the time, namely with regard to the benthic communities. How did the system evolve since then and which were the driving forces behind the observed changes?

The most evident feature was the increase of eutrophication symptoms and its impact on the biological communites, of which the most visible effect was the occurrence of green macroalgae blooms and a concomitant decrease of the area occupied by *Z. noltii* beds. From past observations, we know that disappearance of *Z. noltii* first took place in the inner areas of the south arm of the estuary and went forward to the downstream section, where the distribution of rooted macrophytes is presently limited. In fact, some 20 years ago (Marques et al., 1984), *Z. noltii* beds covered a large part of the intertidal area, extending to the upstream section of the south arm, corresponding to what is now the most eutrophied area. No remains of *Z. noltii* can presently be found here. Nevertheless, in the intermediate eutrophied area, although *Z. noltii* disappeared some time ago, we could still find rests of its rhizomes in the sediment.

Samples collected during 1993 and 1994 provided a valuable data set on the temporal variation of physicochemical factors of water and sediments and of the composition of the benthic communities along the estuarine spatial gradient, allowing to analyse the ongoing process in more detail, since it was possible to monitor the occurrence of a green macroalgal bloom. The way macroalgae extended from upstream to downstream sections in the south arm of the estuary, competing with *Z. noltii*, and the way this process influenced faunal assemblages, illustrated very clearly the impact of eutrophication, that appeared, beyond any reasonable doubt, to be the main driving force behind the ongoing changes in the south arm of the Mondego estuary.

On the other hand, it was possible to produce evidence that, despite nutrient enrichment of estuarine waters due to discharges proceeding from mainland, macroalgae blooms, the main eutrophication symptom, do not occur each year. River management as a function of agricultural practices upstream from the estuary explains why in a plausible way. In fact, the annual variation of *Enteromorpha* spp. biomass was shown to be strongly dependent on the amount of freshwater that enters the south arm during winter and spring (Martins et al., 2001). This is thought to happen according to the following mechanism: (a) a strong freshwater discharge will decrease salinity, and low salinity will inhibit macroalgae growth (Martins et al., 1999), despite the increase in nitrogen in the water column; (b) additionally, dissolved nitrogen discharged from mainland with freshwater will increase N/P ratios, since phosphorous appears to be mostly released from estuarine sediments and becomes diluted in the water column (Martins et al., 2001), which may determine phosphorous limitation in the system. River management emerged, therefore, as a key question in determining secondary scenarios in this eutrophied system, and it appears reasonable to assume that the same might occur in other estuarine systems as well.

One should logically expect that a shift in primary producers could determine changes in other trophic levels (Marques et al., 1997). To a certain extent, this has been illustrated for instance by changes in the population structure of abundant species along the gradient of eutrophication symptoms (Lillebø et al., 1999; Pardal et al., 2000), and by a number of observations and a field experiment on waders carried out in the study area (Cabral et al., 1999; Lopes et al., 2000). But the present results reinforce this notion and indicate

that, through time, the ongoing changes will probably initiate a new trophic structure.

The recent biological changes in the system were tentatively interpreted in the scope of a broad theoretical framework. For that, we enlist the following basic assumption: since *Z. noltii* disappearance in the south arm of the estuary started in the inner areas and progressed downstream, spatial changes in the system may represent temporal changes. In other words, the non-eutrophied area, with *Z. noltii* beds, may represent what the system was two decades ago, the intermediate eutrophied area may represent changing areas during the process, and the most eutrophied area may represent the most advanced stage in the observed shift between primary producers, where the macroalgae has totally ousted macrophytes.

If one accepts this assumption, then the recent modification in primary producers and its related food chain may be seen as a dynamic shift between species. As a consequence, the ecosystem network structure has changed, which may be illustrated by Fig. 7.

In the prevailing conditions two decades ago, rooted macrophytes, *Z. noltii* and related epiphytic grazers dominated by *Hydrobia ulvae* were selected. An important detrital food web was also present.

As eutrophication affected an increasing area of the estuary, green macroalgae, like *Enteromorpha* spp. and *Ulva* spp. replaced the rooted macrophytes. The high turnover of these macroalgae, and the alternation between periods where algae develop high biomasses with periods where bottom sediments are basically bare but rich in organic matter determine an increasing importance of the detritus pathway.

We can now interpret the Mondego estuary processes from a more general viewpoint. Ecosystems exhibit systematic changes in certain parameters as they evolve over a longer time scale, a process known as succession. This term should be reserved to describe the gradual modification of the communities in a relatively undisturbed environment or at least an environment that is imposing only a limited number or size of perturbations on the ecosystem. In such cases the ecosystem will follow a succession during which organisms, populations, and thus the ecosystem as a whole is adapted to meet the long-term average condition of the environment.

More and more often it happens that ecosystems are exposed to disturbances other than the natural ones, which adds an extra stress to the system on top of the natural disturbance level. Such disturbances are often related to human activities and may vary drastically in frequency or orders of magnitude.

The long-term development, succession and modification, of an ecosystem exposed to various degrees of disturbances, natural as well as human caused, may be demonstrated by Fig. 8A. The relation between possible ways of development and concepts from ecological theory are indicated on the corresponding part of the curve. On the left part, at a relatively low level of stress corresponding to normal fluctuations in environmental conditions, we represent a normal succession towards a *climax society*, corresponding to an increase and finally stabilization of the biomass in the system and also its complexity. During this period, the system will follow the traditional developmental patterns as described for instance in the *24 Principles of E.P. Odum*, such as development from r- to K-stragetists, increased cycling, and importance of the network, etc. (Odum, 1971).

With increased stress, often represented by a more frequent occurrence of abnormal events, literature exists that reports an additional stimulation of biomass and diversity, demonstrated by a “hump” on the curve. This may be observed for instance in areas of estuarine systems affected by a certain level of organic pollution and is what is usually referred to as the *intermediate disturbance hypothesis* (Connel, 1978) (Fig. 8A). Meanwhile, this developmental pattern is only thought to be realized in systems with a certain capacity to absorb changing environmental conditions in a constructive manner, i.e. the system has to possess a cache in diversity that is able to react, buffering the disturbances at a larger time scale. This is not always the situation. In case the system has lost or exploited most of its overhead already, either due to natural succession or long-term stress, the possibilities to react properly may be limited or not exist at all. If this is the case, then the system will react with the same response as to an even higher perturbation. In other words, natural succession and/or higher stress forces will lead to “real” macroscopic modification, which takes place through other mechanisms. First of all, continuous adaptation and fine-tuning of parameters leads to a system of highly fitted highly specialized organisms. This in turn will reduce on organism’s ability to respond in a sufficient manner to meet changes

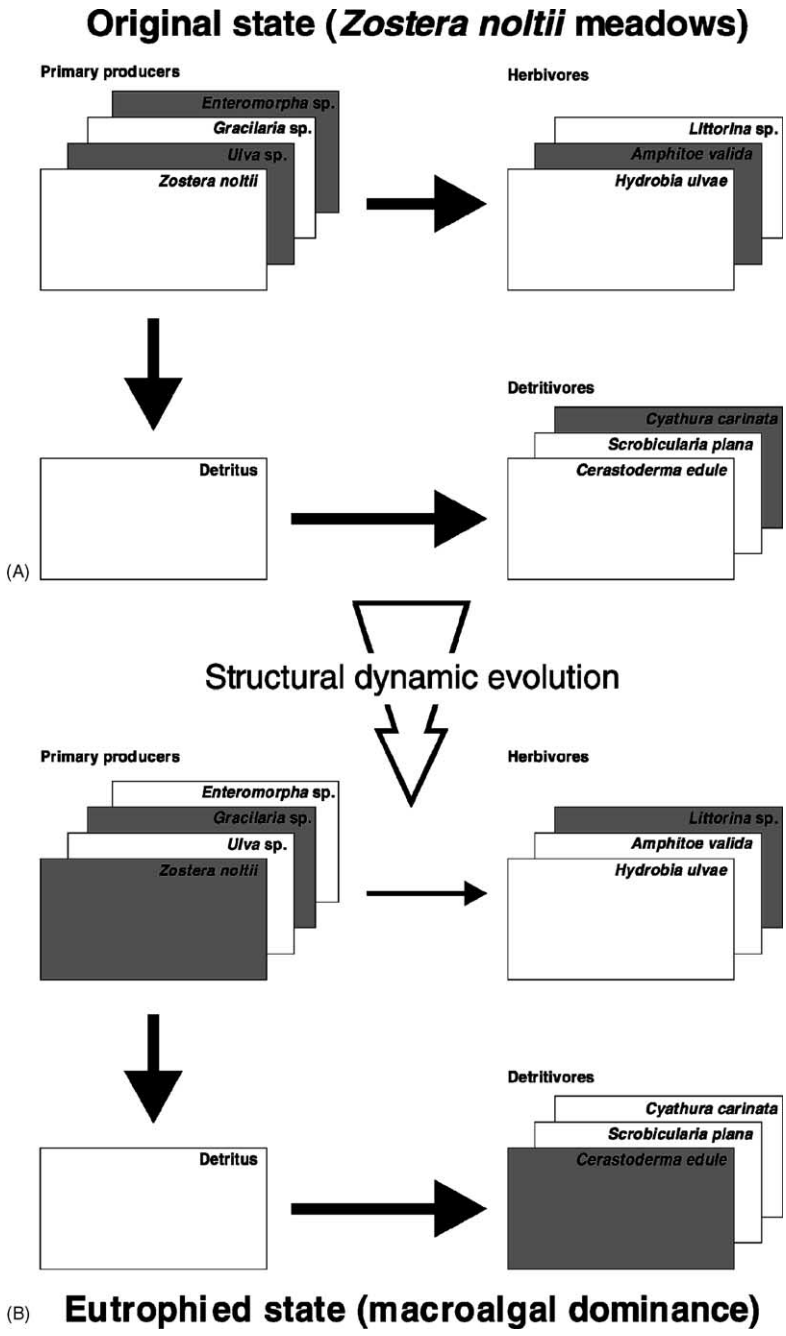

Fig. 7. Structural changes in the trophic network in the south arm of the Mondego estuary as a function of the shift in primary producers induced by eutrophication. (A) Situation at the *Z. noltii* beds, at the non-eutrophied area, assumed to represent the original state of the system. (B) Situation at the most eutrophied area, where macroalgae blooms take place, assumed to represent the new state of the system. Boxes represent species or species aggregations according to their function in the trophic network. White boxes represent the dominant species in each situation, and dark boxes represent species poorly represented. Arrows represent matter fluxes. The width of the arrows reflects the relative importance of the path.

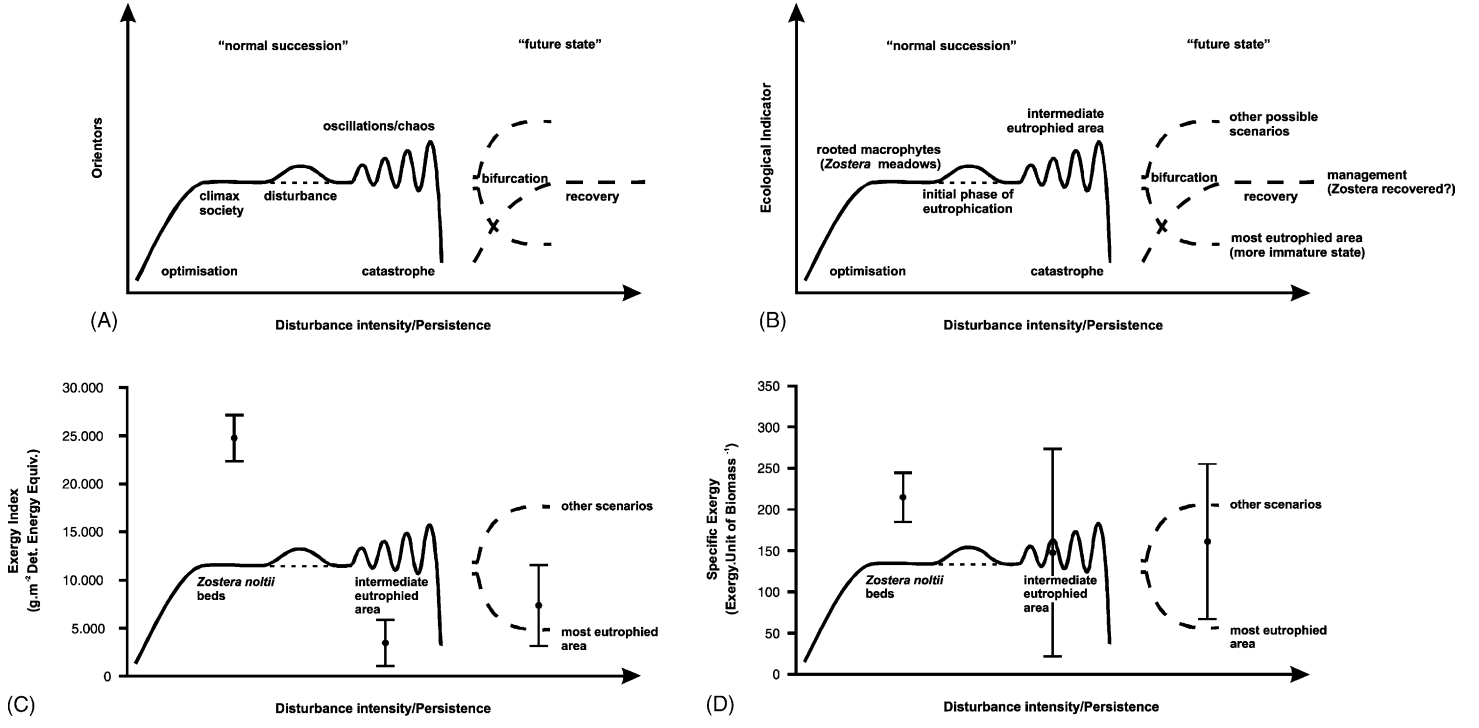

Fig. 8. Orientors (e.g. many of the ecological indicators referred in the literature) development during stress (see for instance Marques et al., 1997). (A) Relation between possible ways of development and concepts from ecological theory are indicated on the corresponding part of the curve. (B) Possible interpretation of changes ongoing in the Mondego estuary in the frame of ecological theory. (C) Spatial variation of the Exergy Index, considering the different areas along the gradient of eutrophication in the Mondego estuary as correspondent to successive stages of the system's recent modifications. Average and standard deviation are indicated, based on data collected from January 1993 to July 1994. (D) Spatial variation of Specific Exergy, considering the different areas along the studied gradient in the Mondego estuary as correspondent to successive stages of the system's recent change. Average and standard deviation are indicated, based on data collected from January 1993 to July 1994.

in environmental conditions. As a result, it is believed that the system as a whole becomes very unstable and brittle (Jørgensen and Johnsen, 1989), which may be expected to correspond to a large short-term fluctuation of an ecological indicators we may use to capture the state of the system (Fig. 8B). Second, adaptation of the network leads to a development where the ecosystem has decreased as much as possible its conditional entropy, or overhead in the sense of Ulanowicz (1986, 1997), i.e. maximizing the utilization of the available resources (energy) through a more and more specialized (efficient) species composition. Such specialization also means a decrease in the possibility of the system to cope with environmental changes, which eventually leads to change through a type of Holling cycle (Holling, 1986; Ulanowicz, 1997).

Moreover, the modification of systems is in non-linear, and as time passes instability gives rise to a bifurcation to new stability points (Glansdorf and Prigogine, 1971) (Fig. 8A and B). In other words, the instability of the system will thus lead it to a breakdown—a *catastrophe*—with possibilities of new organisms and combinations hereof to take over and be selected because the new constellation is better able to meet the prevailing conditions. Catastrophe is here not necessarily used in its narrow mathematical sense and may also not be mathematically as such (Zeeman, 1976). Beyond the point of *bifurcation*, whatever we prefer as interpretation, several possibilities are allowed: (a) A total recovery of the system to an almost identical state can take place, which would correspond to a "normal" understanding and interpretation of the Holling cycle. This of course provided that the perturbation somehow has been stopped, and sufficient biodiversity has been conserved during the stress period to allow the system to return to a quasi-original state. (b) In a case where these conditions are not fulfilled, the system will evolve to one or more stability points, or maybe even continuous instability. The shift to other stability points may also be viewed as if the system is leaving one Holling cycle (Holling, 1986) and entering into another.

Once again, if we accept the above assumption as reasonable, several of these "states" of development can be identified in time and space along the south arm of the Mondego estuary. The recent biological modifications in the estuary and especially its relations to changes in the Pranto River management practices, combined with changes in exploitation of the watershed in agricultural areas upstream from the estuary, introduced additional disturbance and stress to the system.

The following descriptions allow us to understand the present state of each sampling station along the south arm and interpret the situation in accordance with a broader theoretical frame:

(a) The *Z. noltii* beds may be considered as corresponding to the more or less original state of the system, performing with the highest thermodynamic efficiency (Fig. 8C and D), i.e. identical to the climax society demonstrated by the curve (Fig. 8B). Meanwhile, these areas are in regression, showing that they are highly vulnerable to the present conditions.

(b) The most eutrophied area has undergone a transition and, through a bifurcation, found another stability point (Fig. 8B), corresponding to a dominance of green macroalgae, which may or not present blooms as a function of precipitation and river management. This represents a shift from a K- to r-strategy and, in that sense, may be considered as a return of the system to a more immature level. Lower values of the indicators (Fig. 8C and D) appear to support this assumption.

(c) In the intermediate eutrophied area changes exceed the natural variation to a degree where the system is never able to find a new stability point, and the scenario may be placed in the chaotic regime (Fig. 8B). This interpretation is very much consistent to the fact that the highest variations of the indicators are found in this area (Fig. 8C and D). In other words, hydrological conditions act to facilitate in principle colonization by organisms proceeding from both upstream and downstream, but the continuous variation in the disturbances do not allow anymore the system to return to a previous state, when *Z. noltii* was present, neither to reach yet a new equilibrium, like the one observed in the most eutrophied area.

5. Conclusion

Eutrophication appeared, beyond any reasonable doubt, as the major driving force behind the ongoing

changes observed in the south arm of the Mondego estuary, namely the gradual shift in primary producers from a community dominated by rooted macrophytes (*Z. noltii*) to a community dominated by green macroalgae. Concomitant changes at other trophic levels, through time, will likely give rise to a new trophic structure.

River management emerged as a key factor in determining secondary effects in systems already affected by human activities, namely eutrophied systems. Results indicate that much can be done to remediate such areas through more conservative management. We suggest that the cheapest and more realistic way of remediation may the implementation of ecological engineering principles (see for instance Mitsch and Jørgensen, 1989; Jørgensen and Johnsen, 1989) in different possible management practices.

Based on the above knowledge about the system it is clear that two factors play a major role in determining the state(s) of the system. Salinity seems to control the occurrence of macroalgal blooms, whereas nutrient input determines the overall eutrophication state of the system.

To recover the system, i.e. bring it back to its original state of *Zostera* dominance, it seems mandatory to take measures that will improve the present conditions, especially with regard to nutrient level and also water circulation.

Two ecological engineering principles could be implemented fairly easily and at very little costs that would help to improve the present situation and, additionally, in harmonizing two activities that are presently in conflict, respectively aquaculture, in the estuary, and rice production, upstream fish farms. The first would be to exploit the pulsing of the system by synchronizing outlet of freshwater and intake of water for aquaculture with the tides. Second, the establishment of buffering zones, ecotones, in the catchment area should help diminishing the nutrient loads on the system.

In the first case, output of freshwater during outward tidal movement should help to decrease the retention time of nutrients in the estuary. Intake of saltwater for aquaculture necessarily takes place during high tide. Differences in salinity and the resulting density of the overlying water would help to pump out nutrients of the sediments. In the second case, both aquaculture and agricultural activities have to be planned so that nutrient rich waters pass through “constructed” wetlands before entering the estuary directly or via the Pranto River system. For the aquacultures the abandoned Salinas adjacent to the estuary might be used for this purpose and being able to capture most of the organic materials and nutrients of aquaculture origin, and at the same time serve as important habitats to the wildlife, in particular birds. In the case of the rice fields in the Pranto River catchment area, the rice fields, which could be considered constructed wetlands themselves, closest to the river and channels should receive no fertilizers directly but just benefit from the nutrients already in excess in the out flowing surface waters.

The above changes will of course need careful planning, some simple feasibility studies allowing to estimate a dimensioning of the system and plans for management. These measures at the end will most probably turn out to be beneficial to both the socio-economical situation of the farmers and to the environmental state of the Mondego River estuary as well.

From a more general viewpoint, the recent biological modification in the south arm of the estuary may be interpreted in compliance with a broader ecological theoretical framework. Further research will be necessary to understand in a more detailed way processes involved. The development of a structurally dynamic model able to describe the shift in the communities as a function of environmental changes will represent a strong tool with regard to this purpose.

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